THE DEVELOPMENT OF THE ASCOCARP OF LEOTIA[1]

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(WITH FORTY-SEVEN FIGURES)

The present study is based upon material of *Leotia lubrica* and *L. chlorocephala* collected at Cold Spring Harbor, Long Island. For microscopical study, sections were cut 2 and 3 μ thick and stained with either Haidenhain's iron-alum hematoxylin or Flemming's triple stain.

Leotia lubrica

Leotia lubrica grows in damp places among various species of mosses. Several ascocarps are often connected together by their bases, and sometimes a small one may grow out from the base of a mature specimen.

The age of an ascocarp cannot always be told from its size, for one 3 mm. long may be more mature than one about 1 cm. in length. The youngest specimens found were about 1.5 mm. long, and were nearly conical in shape (fig. 1). When the ascocarp has reached a length of about 2 mm., the tip of the cone begins to enlarge to form the head (figs. 2, 3); this is about the stage at which the hymenium begins to be differentiated. The ascocarp soon assumes the mature form (fig. 4), and the further changes are largely those of growth. The hymenium now covers the upper surface and margin of the head. The upper surface may continue to grow until its margin becomes curved in toward the stalk (fig. 5).

The youngest specimen found was composed largely of densely interlacing vegetative hyphae. At the base of the ascocarp there was a very large cell (fig. 6) from which a number of large hyphae extended upward toward the tip of the ascocarp. This large cell was vacuolated and its contents had degenerated, giving it all the appearances of an emptied ascogonium. The hyphae arising from this cell were empty, as is usually the case in old ascogenous hyphae, and so could not be traced with certainty for any great distance.

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They appear, however, to be connected with similar hyphae which become very distinct only a little farther up (about 10 μ) in the ascocarp. These latter hyphae, of which there are three or four, are the ascogenous hyphae. They are very much larger than the surrounding vegetative hyphae, and in the character of their contents are quite distinct from them. The ascogenous hyphae become more and more distinct as they get nearer the tip of the ascocarp, but they show little tendency to branch until they have reached about one-half the distance from the base to the tip, when they divide to form a large number of smaller, much branching hyphae. These latter hyphae have a tendency to spread out as well as to grow upward, but in young specimens they are of course near the larger hyphae. Assuming that the large cell at the base of the ascocarp is an ascogonium, as seems to be the case, and that it is connected with the ascogenous hyphae, this stage may be represented diagrammatically as in fig. 7, in which the black lines represent the ascogenous hyphae. In slightly older specimens the ascogenous hyphae have spread over the entire tip. At about this time the tip enlarges to form the head of the ascocarp. Some of the vegetative hyphae soon grow out to form the paraphyses, after which the ascogenous hyphae give rise to asci. This stage is represented diagrammatically in fig. 8, in which the black lines still represent the ascogenous hyphae, the older parts of which have disappeared.

While the hymenium is being differentiated, some of the vegetative hyphae give rise to large storage cells (fig. 9). This process is similar in the two species studied and the same description will apply to both. These large storage cells are formed in rows and give rise to paraphyses (fig. 10). The storage cells are at first multinucleate, but the nuclei usually fuse as growth proceeds (figs. 11–14). This process continues until often the cells contain a single, very large nucleus, many times the size of the largest nucleus in the ascus (figs. 15–17). Frequently the nuclei are very irregular (fig. 18). In other cases, a cell may contain a very large nucleus with several much smaller ones lying near it (fig. 19). These last two cases suggest amitoses, but may very well be stages in fusion. The storage cells may have a very irregular shape

(fig. 20), or they may be quite regular (fig. 17). They are relatively much more abundant in young ascocarps than in the older ones. The storage cells seem to have the same function as the barrel-
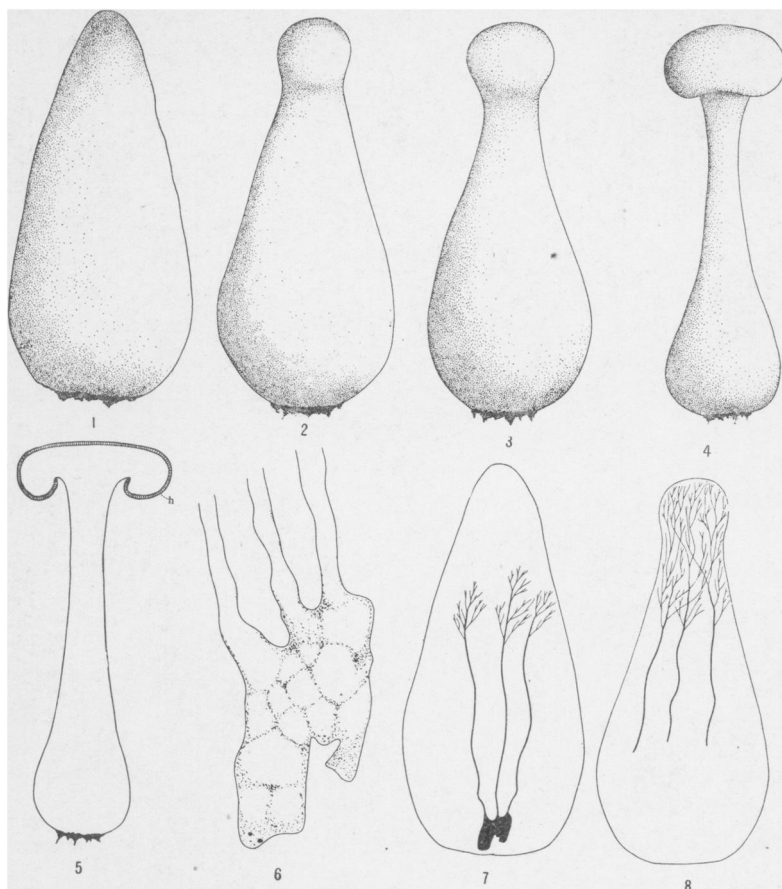
FIGS. 1–8.—Fig. 1, young ascocarp, ×50; fig. 2, early stage in formation of head, ×37; fig. 3, older stage, ×30; fig. 4, mature ascocarp, ×3; fig. 5, longitudinal section of old ascocarp (h, hymenium), ×2.5; fig. 6, large cell at base of ascocarp, ×2100; fig. 7, diagram showing probable relation of ascogenous hyphae and ascogonium in young ascocarp; fig. 8, diagram showing position of ascogenous hyphae at time of formation of hymenium.

shaped cells described by HARPER (16) in *Pyronema confluens*, and are very much like similar storage cells in *Lachnea scutellata*. The chief difference seems to be that in *Pyronema confluens* and
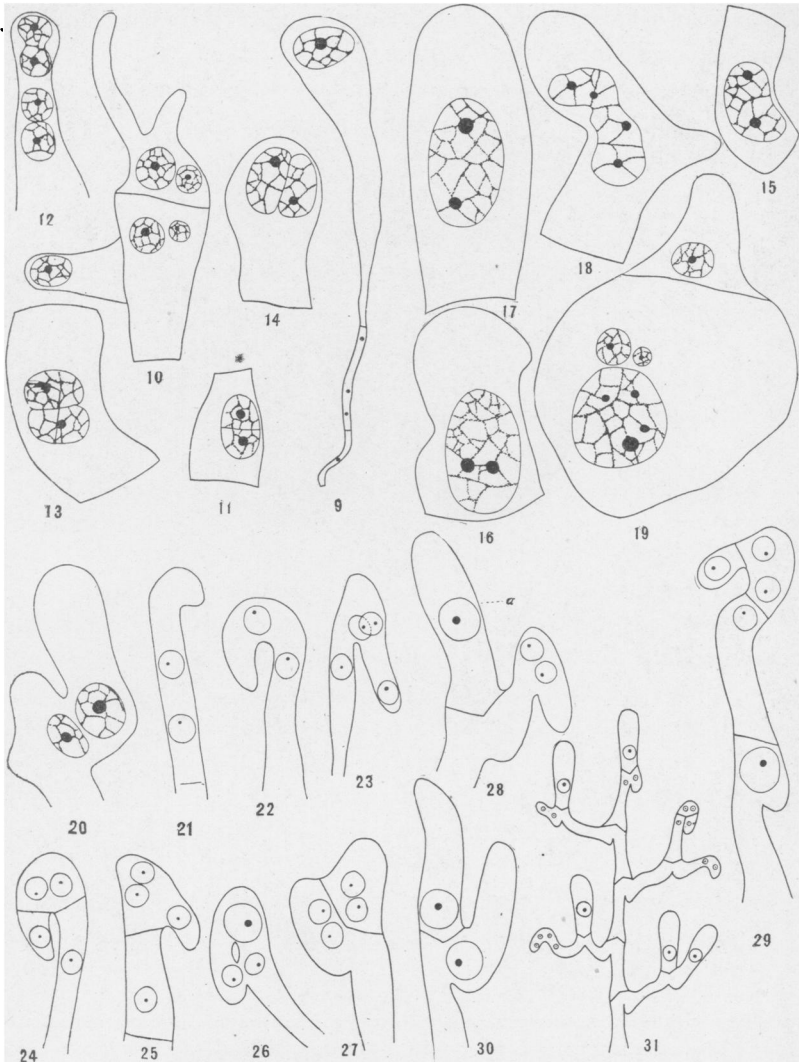
FIGS. 9–31.—Fig. 9, vegetative hyphae giving rise to storage cell; fig. 10, paraphyses growing out from storage cells; figs. 11–14, fusion of nuclei in storage cell; figs. 15, 16, nucleus with two nucleoli in storage cell; fig. 17, large storage cell with single very large nucleus; fig. 18, storage cell with very irregularly shaped nucleus; fig. 19, storage cell containing one large and two small nuclei; fig. 20, an irregularly shaped storage cell; figs. 21, 22, tip of ascogenous hypha with two nuclei; fig. 23, two nuclei in tip of hypha have divided to four; fig. 24, walls have come in, separating sister nuclei; fig. 25, hook in which there is no wall cutting off uninucleate ultimate

Lachnea scutellata the nuclei of the storage cells probably do not usually fuse.

The details in the formation of the asci were studied chiefly in *Leotia chlorocephala*, and will be described in connection with that species.   The appearance of the hymenium suggests, however, that the process is similar in the two cases.

Leotia chlorocephala

The ascogenous hyphae in *Leotia chlorocephala*, as in *L. lubrica*, have their origin in the stipe.   The hymenium is also formed in the same way that has been described for *L. lubrica*.

In 1894 DANGEARD described the asci of *Peziza vesiculosa* as originating from a binucleate penultimate cell of an ascogenous hypha.   Since that time the same phenomenon has been described by various workers in a number of forms.   A large number of these are mentioned by OVERTON (**23**).   The usual case seems to be that there are two nuclei in the tip of an ascogenous hypha.   These divide simultaneously and walls come in between the sister nuclei of the two pairs, thus forming a binucleate penultimate cell and a uninucleate ultimate and antepenultimate cell.   The ascus is then formed from the binucleate penultimate cell.   MAIRE (**20**) and GUILLIERMOND (**14**) have described the asci of *Galactinia succosa* as originating from a binucleate ultimate cell.   In *Humaria granulata* (BLACKMAN and FRASER **4**) the asci usually arise from a binucleate penultimate cell, but in two cases the asci had a terminal position.

In speaking of *L. chlorocephala* and a number of other ascomycetes, FAULL (**11**) says: "It is quite probable that the only

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cell; fig. 26, hook in which two nuclei have fused to form nucleus of ascus, and tip has fused with stalk of hook; fig. 27, ultimate cell has fused with antepenultimate; nucleus of latter has migrated into former, which is growing out to give rise to ascus or another hook; fig. 28, two nuclei of penultimate cell have fused to form nucleus of ascus; ultimate cell has fused with antepenultimate, and nucleus of latter has migrated into former, which has grown out to form another hook; fig. 29, binucleate penultimate cell has given rise to hook; ultimate cell has fused with penultimate, and the two nuclei have fused; ultimate cell has not developed further; fig. 30, binucleate penultimate cell has formed ascus, which fusion product of ultimate and antepenultimate has given rise to second ascus; fig. 31, diagram illustrating multiplication of number of asci by method shown in figs. 26–30; figs. 9–20, ×1400; figs. 21–30, ×2100.

departure from the type is the lack of the cross wall that cuts off a uninucleate cell at the tip of the hypha." Later on he says that in some of the species the cross wall may be exceptionally present. In this statement he probably includes *L. chlorocephala*, as the cross wall is frequently present in this species. *L. chlorocephala*, however, shows quite a number of other deviations from what has been regarded as the usual type.

The tips of the ascogenous hyphae in the hymenium usually contain two nuclei, and become shaped like a hook (figs. 21, 22). The nuclei then divide, giving rise to four nuclei (fig. 23). Walls may then come in between the sister nuclei (fig. 24), or the wall cutting off the terminal cell may not be developed (fig. 25), or in still other cases both walls may be lacking even after the two nuclei in the bent portion of the hook have fused to form the nucleus of an ascus (fig. 26). When the nuclei are distributed as in figs. 23, 24, so that one is in the tip and two in the bent part of the hook, the two nuclei (apparently not sisters) in the bent portion may fuse to form the nucleus of an ascus (figs. 26, 28*a*), or they may give rise to the four nuclei of another hook (fig. 29). The uninucleate tip usually grows down and fuses with the stalk of the hook (fig. 26). The nucleus of the stalk may then migrate out into the tip (fig. 27), which usually grows out to form another hook (fig. 28), or sometimes an ascus (fig. 30). That in these cases it is the tip which has developed below the ascus is shown by the presence of the curved end of the tip joined to the stalk cell, as well as by the presence of both the wall which separated the ultimate cell from the penultimate and the one which divided the penultimate from the antepenultimate. The nucleus from the tip of a hook may occasionally migrate into the stalk. Sometimes the nucleus formed by the fusion of the nuclei of the tip and stalk does not develop further (fig. 29). This is usually associated with a vacuolated condition of the cytoplasm which indicates that the failure of the tip to develop is due to a lack of food. The processes described above, by which either the tip or bent portion of a hook may form another hook, are apparently often repeated many times, so that even in a young stage of the hymenium five or six hooks are frequently seen joined together in various ways. This is shown diagrammatically in fig. 31.

This same method of multiplication of asci occurs in *Geoglossum* sp. (figs. 32–38). The two nuclei in the tip divide to four (fig. 32) and walls come in between the nuclei of each pair of sisters (fig. 33). The antepenultimate cell may then form an ascus (figs. 37, 38) or another hook (figs. 35, 36). The ultimate cell usually fuses wlth the stalk (figs. 34, 35). The nucleus of the ultimate cell may then migrate into the antepenultimate (fig. 35), but usually the nucleus of the antepenultimate cell migrates into the ultimate (fig. 34), which then grows out (fig. 36) to form a hook (figs. 37, 38) or an ascus.

The phenomena connected with the formation of the asci as just described in *Leotia* and *Geoglossum* have been observed by the writer in *Lachnea scutellata*, as reported before the Botanical Society of America at the 1909 meeting (6). In a paper read at the same time before Section G of the A.A.A.S., McCubbin (21) described the penultimate cell of the ascogenous hyphae of *Helvella elastica* as forming either an ascus or a hook. The ultimate cell frequently fuses with the antepenultimate, after which the nucleus of the antepenultimate migrates into the ultimate. The two nuclei then migrate into a process which grows out from the ultimate to form another hook. In *Humaria rutilans* Miss Fraser (12) has described the uninucleate ultimate cells of the ascogenous hook as growing out to form other asci. She says that where such proliferation had taken place the tip was usually connected with the stalk, and in one case the nucleus of the tip was migrating into the stalk. She did not determine, however, whether or not the nucleus of the stalk took part in the formation of new asci. It seems probable, however, that she has observed something of the same phenomenon that has been described in *Leotia*. The writer (5) has described the ultimate cell of *Pyronema confluens* as growing out to form other asci. In such cases a nucleus could not be found in the stalk cell, and so it may be that it had migrated into the ultimate cell and had then taken part in the formation of the hook. The presence of these phenomena in such rather distantly related species as those mentioned above suggests that they may be of rather frequent occurrence.

Remembering that the nuclei in the binucleate antepenulti-
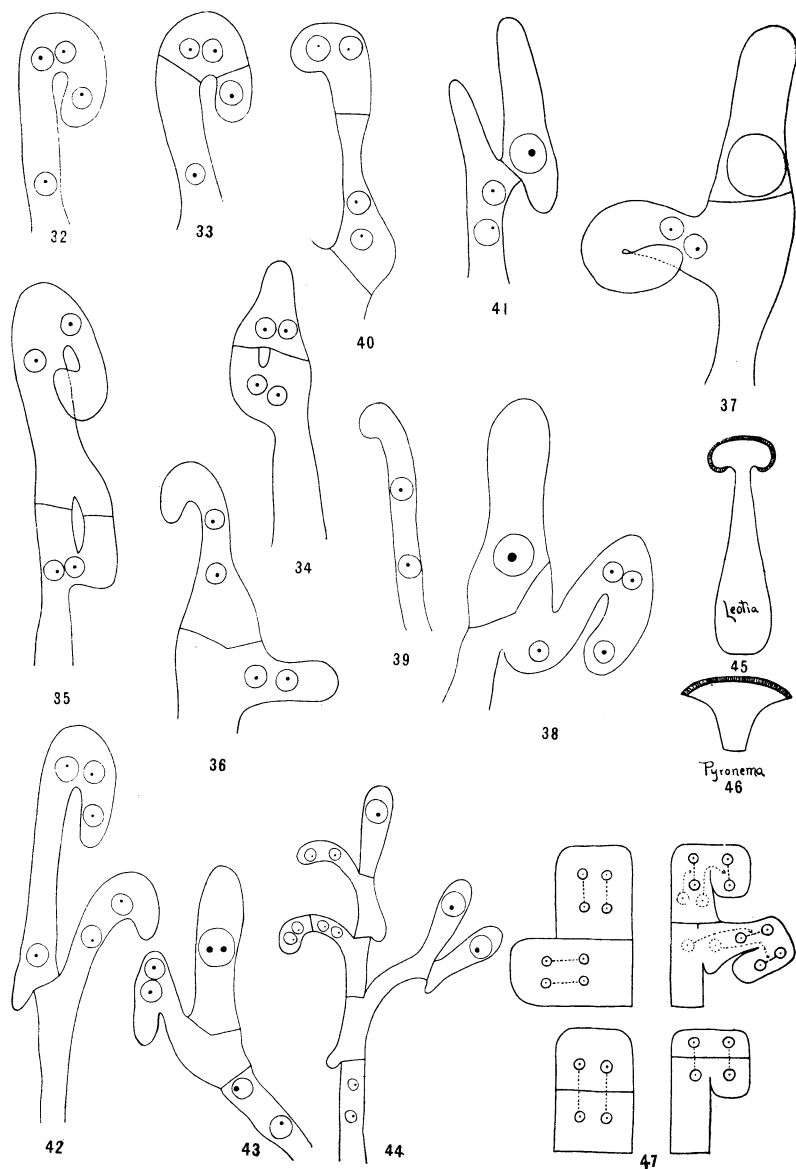
FIGS. 32–47.—Figs. 32–38, *Geoglossum* sp.; fig. 32, four nuclei in tip of hook; fig. 33, walls have come in between nuclei; fig. 34, ultimate cell has fused with stalk; fig. 35, binucleate penultimate cell has given rise to hook, while ultimate has fused with antepenultimate; fig. 36, binucleate penultimate cell has formed hook, and ulti-

mate cell are not sisters, but are composed of one nucleus from each of two pairs of sisters, it will be seen that every time either the ultimate or penultimate cell, if formed in the manner described above, gives rise to a hook, the distance of the relationship of the nuclei which fuse to form the nucleus of the ascus is increased. This can hardly be of any significance, however, in the case of *L. chlorocephala*, for, as will be shown later, two nuclei which are apparently sisters often fuse to form the nucleus of an ascus.   It seems probable, therefore, that in *Leotia* the only use of the continued growth of the ultimate and penultimate cells is to increase greatly the number of asci which can be formed from a single hypha.

 In *L. chlorocephala* the asci are also formed by another method, which probably occurs about as frequently as the one already described.   In this case the tip of the hypha does not bend as much as in the first (fig. 39).   When the nuclei have divided, a wall comes in between the two pairs of sister nuclei (fig. 40).   That the two nuclei in each cell are sisters would seem to be shown by the fact that the hyphae appear to be too narrow to allow a side-by-side division of the nuclei, or for the nuclei to migrate past each other.   There is, moreover, no evidence that such a parallel division or migration of the nuclei does occur.   The two nuclei of the ultimate cell may fuse to form the nucleus of an ascus (fig. 41), or they may give rise to the four nuclei of another hook (fig. 42).   That the asci and hooks in these cases are formed from a binucleate terminal cell is shown by the presence of the tip of the

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mate has grown out; figs. 37, 38, binucleate penultimate cell has formed ascus, while ultimate with nucleus from antepenultimate has given rise to hook; fig. 39, tip of ascogenous hypha with two nuclei; fig. 40, the two nuclei have divided to four and a wall has separated the two pairs of sister nuclei; fig. 41, two nuclei of ultimate cell have fused to form nucleus of ascus; penultimate cell is growing out to give rise to hook or ascus; fig. 42, both ultimate and penultimate cells have formed hooks; fig. 43, penultimate cell (*a*) has not developed further, while ultimate has given rise to hook similar to that shown in fig. 24; binucleate penultimate cell of this hook has formed ascus, while ultimate and antepenultimate have given rise to still another hook; fig. 44, diagram illustrating multiplication of asci by method shown in figs. 39–43; fig. 45, diagram of structure of ascocarp of *Leotia;* fig. 46, diagram of structure of ascocarp of *Pyronema omphaloides;* fig. 47, diagrammatic comparison of conjugate divisions in *Leotia* and in the rusts; figs. 32–43, ×2100.

hook at their bases. The binucleate penultimate cell may also grow out (fig. 41) to form a hook (fig. 42), or sometimes an ascus. In other cases it does not develop further (fig. 43). When this occurs the two nuclei may or may not fuse. Fig. 43 shows a case in which two binucleate cells were formed, the terminal one of which developed into a three-celled hook of the type first described. This hook then gave rise to an ascus and a second hook. It is clear from this that the same hypha may behave differently at different times. The formation of two binucleate cells may be repeated several times, as is shown diagrammatically in fig. 44.

In *Verpa bohemica*, FAULL (11) found the asci connected with the first, second, third, or fourth cell from the tip, but did not determine whether the asci grew out from the third or fourth cell, or whether the terminal cell underwent division after the budding out of the ascus.

In *Anixia spadicea* and *Urnula craterium*, FAULL (11) says that it looks as if the ascus might spring from any cell whatever. Judging from FAULL's figures, all of the above cases might perhaps be explained as due to the two methods of multiplication of asci described in *Leotia*.

In *L. chlorocephala* the ascus soon after its formation grows out into a much elongated cell. Its nucleus divides three times, in the manner usual among the nearly related Pezizineae, and gives rise to the nuclei of the eight spores. The spores are at first round, but by subsequent growth they become elongated and vacuolated.

Systematic position of Leotia

ENGLER (10) places *Leotia* in a group near the Pezizineae. The observations recorded above seem to confirm this view of the near relationship. The large cell, probably an ascogonium, at the base of the ascocarp and the presence of the ascogenous hyphae in the stipe suggest a homology with those Pezizineae in which the asci are formed from a single ascogonium, as *Lachnea scutellata*, *Peziza granulosa*, *Ascobolus pulcherrimus* (WORONIN 29), *Ascobolus furfuraceus* (JANCZEWSKI 17, HARPER 15, WELSFORD 28), *Ascodemus nigricans* (VAN TIEGHEM 27), *Ryparobius* sp. (BARKER 1),

Thelebolus stercoreus (RAMLOW **24**), *Humaria granulata* (BLACK-
MAN and FRASER **4**), *Lachnea stercorea* (FRASER **13**), and *Asco-
phanus carneus* (CUTTING **7**).

As has already been pointed out, the origin of the hymenium,
including the storage cells and the formation of the asci, is also
similar to the same process in some of the Pezizineae.

The presence of an elongated stipe, moreover, is of frequent
occurrence among the Pezizineae, while a tendency of the hymenium
to become recurved is shown by many of them. A comparison
of figs. 45 and 46 will show the similarity in form between *Leotia*
and an old specimen of *Pyronema confluens*.

From the above considerations it would seem that *Leotia* is
as closely related to some of the Pezizineae as some of them are
to each other, and it is probable that the ancestors of *Leotia* were
closely similar to some of them.

Relationship of the fusing nuclei

According to what is probably the most prevalent interpreta-
tion, the fusion in the ascus is regarded as being of a vegetative
character, and so the relationship of the fusing nuclei is considered
to be of no great significance. This interpretation is based on the
presence of a supposed fusion of nuclei in the ascogonium. Such
fusions have been described in *Pyronema confluens* (HARPER **16**),
Humaria granulata (BLACKMAN and FRASER **4**), *Lachnea stercorea*
(FRASER **13**), *Ascobolus furfuraceus* (WELSFORD **28**), *Humaria
rutilans* (FRASER **12**), and *Ascophanus carneus* (CUTTING **7**).
CLAUSSEN (**8**), however, after a study of *Pyronema confluens*, has
come to the conclusion that the fusion in the ascus is the only one
that occurs in that species. BROWN (**5**) has described a form of
Pyronema confluens in which the antheridium does not fuse with
the ascogonium, and in this case he fails to find a fusion of nuclei
in the ascogonium. The cytology of the ascus confirms this inter-
pretation. There are, however, appearances in this form very
much like fusing nuclei, which are due, however, to the fact that
the daughter nuclei reorganize close together. BARKER, in studying
Monascus, failed to find a fusion of nuclei in the ascogonium, but
attributed this to his failure to get the proper stages. SCHIKORRA

(25) describes the fusion of the antheridium and ascogonium in *Monascus*, but does not find any fusion of nuclei except in the ascus. In *Lachnea scutellata* the writer has been unable to find any fusion of nuclei except the one in the ascus. The haploid number of chromosomes persists throughout the vegetative hyphae, ascogonium, and ascogenous hyphae; while the diploid number exists only in the primary nucleus of the ascus. There are, however, appearances in the ascogonium and other parts of the ascocarp, which were at first mistaken for fusing nuclei. When the nuclei are preparing for division, the chromosomes tend to become arranged in a group resembling a nucleolus. The nuclei at this stage are of course large, and often, unless well stained and carefully studied, appear to have two nucleoli. When the nucleoli have divided, they often reorganize so close together that after a slight growth they are pressed against each other as in the case of fusing nuclei. Careful study, however, has failed to show any cases in which the nuclear walls were disappearing, and often the remains of spindle fibers could still be distinguished. Even the nuclei resulting from the division of the primary nucleus of the ascus can sometimes be found pressed against each other. Considering the above facts and the increasing amount of negative evidence, it would seem necessary to study the nuclei in all stages, including division, and to distinguish between true and apparent fusions before the fusion of nuclei in the ascogonium can be regarded as proved or even probable. This is particularly true of such an aberrant case as the presence of a second nuclear fusion following the sexual fusion in the life history of the same plant, and it is to be noted that divisions in the ascogonium have not been reported in any of the forms, mentioned above, in which a fusion of nuclei has been described in the ascogonium. In view of what has been said, there would seem to be little reason for thinking that *Leotia* differs from *Monascus* and *Lachnea scutellata* in having a fusion of nuclei in the ascogonium; and so the explanation of the fusion of sister nuclei will probably have to be sought in some other way than by regarding the fusion as simply a vegetative one.

The question may be asked as to whether the relationship of fusing nuclei is of any significance if they are in the same plant

and are derived from a single nucleus with the haploid number
of chromosomes.   So far as the writer knows, there is no reason
for thinking that there is.   It is well known in agriculture that
self-fertilization causes a diminution in the size and vigor of maize.
SHULL (26) has shown that ordinary maize is a complex hybrid.
If the elementary species are segregated out of the hybrid, self-
fertilization has no bad effect, and it would seem that the deteriora-
tion of agricultural maize after self-fertilization is due to the
segregating out of the smaller elementary species, which when
recombined will again produce the more vigorous agricultural
variety.   According to the Mendelian interpretation, the harmful
effect of self-fertilization in other genera is due to the same cause.
The value of cross-fertilization for evolution is evident when we
remember that it affords a means for trying a new character in a
great number of combinations, one of which may finally be espe-
cially adapted to its environment.   It may be that the persistence
of cross-fertilization is due to its value in evolution, and that the
presence of self-fertilization in such a relatively small number of
the higher plants is due to the fact that such plants had less chance
to interchange characters by crossing and so to develop along
favorable lines.

It is evident that the above beneficial effects could not be
produced by the fusion of distantly related nuclei if these were
all in the same plant and were derived from a single nucleus with
the haploid number of chromosomes, for even if the potentialities
of one of the fusing nuclei were to be changed in some way, the
change would probably be inherited by only one-half of the result-
ing progeny, and the nuclei of these would have the same poten-
tialities as the changed nucleus and there would be no chance for
further mixing.   The end result would be the same if the nucleus
whose potentialities had been changed had divided, and the two
daughter nuclei had fused and given rise to the progeny.   But
even if a change in the fusing nuclei could be thought of as bene-
ficial, there is no reason for thinking that such a change would
occur.   The work of JENNINGS (18) and JOHANNSEN (19) seems
to show that the germ cells of organisms derived from a single
pure individual are very rarely affected, even if the organisms

are subjected to different conditions and a rigorous selection practiced. In view of what has been said, we would not expect the relationship of fusing nuclei to make any difference if they were all in the same plant, and especially if they were all derived from a single nucleus with the haploid number of chromosomes. When therefore the ascogonium and antheridium, as in *Pyronema confluens* (HARPER 16), came to be derived from a single hypha, it would not seem to be a matter of great significance if the fusion of the nuclei derived from the ascogonium and antheridium should be replaced by the fusion of more nearly related or even sister nuclei, as seems sometimes to be the case in *Leotia chlorocephala*. It may be that the tendency toward the loss of sexual organs which is shown by a large number of the higher fungi is connected with the fact that there is in so many of them no provision for the fusion of nuclei derived from different individuals.

Conjugate division

In the first process of multiplication of asci described in *Leotia chlorocephala* there is a series of conjugate divisions comparable to those in the rusts. When the hook gives rise to a binucleate penultimate cell and a uninucleate ultimate and antepenultimate cell, and then the ultimate cell fuses with the antepenultimate, there result two binucleate cells in which the two nuclei are derived one from each of two pairs of sisters. This is of course the relation that exists in the rusts. The processes in the rusts and in *Leotia* are compared diagrammatically in fig. 47. If in *Leotia* the nuclei divided side by side rather than one in the tip and the other nearer the base of the hypha, and the walls still came in between the sister nuclei, there would result a series of binucleate cells resembling very closely those in the rusts. Such a division in an ascomycete has been described by MAIRE (20) in *Galactinia succosa*.

The cells which fuse in the rusts are often derived from separate hyphae, but BLACKMAN (3) says that in some cases the fusing cells may be sisters, while OLIVE (22) figures two cases in which one nucleus is apparently migrating into an adjoining cell. The fusion of the ultimate and antepenultimate cells in the hooks of

the Ascomycetes is probably vegetative, and its replacement by the fusion of cells of separate hyphae or sister cells would give rise to a process quite similar to that in the rusts. While the above facts suggest a similarity between the Ascomycetes and the rusts, they do not appear to be sufficient to warrant the conclusion that the fusions and conjugate divisions in the two groups are phylogenetically related.

Summary

The ascogenous hyphae of *Leotia* have their origin at the base of the ascocarp, probably from a one-celled ascogonium.

The asci are formed at the tips of the ascogenous hyphae in several different ways. In some cases a hypha forms a typical hook, consisting of a binucleate penultimate and a uninucleate ultimate and antepenultimate cell. In this case the two nuclei of the penultimate cell may fuse to form the nucleus of an ascus, or they may divide and give rise to the four nuclei of another hook. The uninucleate ultimate cell usually grows down and fuses with the antepenultimate cell, after which the nuclei of the two cells may give rise to the nuclei of another hook, or they may fuse to form an ascus. The walls separating the nuclei may fail to be formed without affecting the fate of the nuclei. In this process there is a conjugate division comparable to that in the rusts.

Frequently the ascogenous hyphae do not become markedly bent, and in this case, when the two nuclei in the tip divide, a wall may separate two pairs of sisters. Either of these pairs may divide and give rise to the nuclei of another hook or fuse to form the nucleus of an ascus. Any of the methods described above by which the number of asci is increased may be repeated many times.

The relationship of the nuclei which fuse in a plant like *Leotia* is probably of no significance, since they are all in the same plant and are probably derived from a single nucleus with the haploid number of chromosomes.

The vegetative hyphae form large storage cells in the hymenium. The nuclei in these cells frequently fuse to form a single large nucleus.

The development of the ascocarp indicates that all of its struc-

tures are homologous with those of the Pezizineae, and that *Leotia* is closely related to the Pezizineae.

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